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## A Macroscopic and Microscopic Study of the Mental Hedonic Gland-clusters of Some Plethodontid Salamanders

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ABSTRACT. The mental hedonic gland-cluster is a small patch of glands located near the tip of the chin of most, if not all, male plethodontid salamanders. The structural relationships of the gland-clusters of several species of Mexican and South American plethodonts were investigated. Both macroscopic and microscopic morphology are discussed. Reference is made to the origin and function of the glands.

Structural characteristics indicate that the gland-clusters present in the genus *Oedipina* are the most specialized, while the clusters found in the genera *Pseudoeurycea*, *Chiropterotriton*, *Bolitoglossa*, *Magnadigita* and *Thorius* display lesser degrees of specialization.

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## INTRODUCTION

A small cluster or patch of glands is found on or near the tip of the chin of most, if not all, species of plethodontoid salamanders. This cluster is usually evident as a small oval, circular, cordiform, or somewhat triangular structure, slightly elevated and generally differing in color from that of the surrounding skin. This cluster of glands, which occurs only in males, is obviously a secondary sexual character, since previous studies have shown that the glands function during the breeding season in some manner so as to stimulate the female into activity during courtship. These glands have been referred to by certain authors as hedonic glands, but since this name has been utilized in a general way, the patch of glands is here designated as the mental hedonic gland-cluster.

The character of this cluster of glands has been ascertained in many of the North American plethodontoid genera, but only a most superficial examination of it has been made in those genera occurring in Mexico and Central America. The purpose of this paper, therefore, is to describe the glands in several genera of Mexican and South American plethodontoid salamanders, and also to interpret any evidence of relationships among the genera and species examined as indicated by the cluster.

## METHODS AND TECHNIQUES

Two methods were used in this investigation to achieve the desired results. The following is a description of these methods.

*Macroscopic.* The cluster of glands which is embedded in the skin immediately posterior to the symphysis of the mentomeckelian bones at the anterior angle of the lower jaw was exposed by cutting the skin loose from the bone and pulling the skin backward from the snout. This exposed the cluster so that it could be studied *in situ* or removed for sectioning. Several attempts were made to stain the glands *in toto*, but some difficulty was encountered, so that this procedure was abandoned and unstained whole mounts were substituted. For observation, the skin flap containing the cluster of glands was pulled to one side and examined over a dark background with a binocular dissecting microscope. Using this technique it was possible to determine the number of glands, their shape and approximate size, and their arrangement within the cluster. Relatively accurate measurements of the entire cluster were also possible. The cluster was either placed directly over a rule, or was measured with calipers. It is possible that there was a slight error in counting

the number of glands in each cluster, because in many instances they were irregular in size and shape, and there was some overlapping of the individual glands. The measurements of thickness of any cluster includes the limiting membrane of connective tissue as the internal border and the epidermis as the external border. The epidermis is included in these measurements because microscopic examination revealed that the external pores were at the external surface of the epidermis.

*Microscopic.* Microscopic studies were made of the clusters of several species. Only mature males were used. All the specimens used in this investigation had been killed and preserved for museum study several years previous to this investigation, and as a consequence the degree of fixation was not constant throughout the series. All the specimens had been preserved in formalin and transferred to 70 per cent alcohol.

A skin flap containing the cluster of glands was obtained in the same manner as for the macroscopic examination, except that for microscopic studies the cluster was removed. Usually a portion of the skin surrounding the cluster was left attached to the cluster so that comparisons could be made between the hedonic glands and the mucous glands located throughout the skin. The clusters were then placed in fresh 70 per cent alcohol, run in consecutive steps up to 100 per cent alcohol, and transferred into zylene. From the zylene they were transferred to mixtures of zylene and paraffin and then into pure paraffin. They were embedded in pure paraffin and placed in a refrigerator to harden. Sections were cut at 6-8 microns, transferred to microscope slides, attached with egg albumen, and allowed to dry for 24-48 hours before staining.

Several stains were used experimentally but the stain found to produce the best results was Mallory's Triple stain (1921, p. 219). The technique used in staining is that prescribed by Guyer (1921, p. 219).

#### ACKNOWLEDGMENTS

I wish to thank Dr. Edward H. Taylor, under whose direction this study was pursued, for the use of his large collection of plethodontid salamanders, many of which are discussed in this paper, and also for the time and energy he has expended in helping with the preparation of this paper. I wish to also thank Dr. A. Byron Leonard for his kind assistance in describing some of the microscopic structures found in this investigation.

PREVIOUS INVESTIGATION OF STRUCTURE  
AND FUNCTION OF THE GLANDS

Most of the experimental work pertaining to the hedonic glands has been concerned with function rather than with structural relationships; however, such work as has been done on the structure has been excellently recorded by several authors.

Noble (1921, p. 4), describes the hedonic glands of *Eurycea bislineata* as having a central lumen bordered by tall columnar cells, with a finely granular or pasty cytoplasm. The cells stain bluish-purple in Mallory's stain and pink in hemotoxylin.

Smith (1941, p. 259), in describing the hedonic glands of *Triturus torosus* states that during the height of development the gland may contain several types of cells, and that they are chiefly columnar, with elliptical nuclei so oriented that the long axis is parallel to that of the cell, and that although a few of the nuclei appear pyknotic, most of them stain similarly to those of the surface epithelium. Smith further states that the cytoplasm contains small basophilic and a few refractile granules, and at the height of development the central part of the hedonic gland is crowded with cells. He believes that the gland is of the holocrine type, because the granular epithelium is usually destroyed during the elaboration and expulsion of the glandular product. He states also that the glands are surrounded by what is apparently a myo-epithelial capsule which may be instrumental in the discharge.

Noble (1929, p. 4), in describing the hedonic glands of *Eurycea bislineata*, states that the gland on the dorsum of the base of the tail is large, but is not visible externally in the living animal. The glands on the sides of the body and on the legs are also generally invisible externally in the living animal. The glands on the eyelids and in the temporal region have also been shown to be hedonic glands. Noble (1929, p. 4) states also that microscopic sections of the female of the same species showed no evidence of hedonic glandular tissue anywhere on the head, body, or tail.

"Hedonic glands of the type found in *E. bislineata*," continues Noble (1929, p. 4), "are of general occurrence in the *Plethodontidae*, and homologous structures seem to occur in *Salamandridae*. They appear as visible structures on the lower eyelids of the male *Desmognathus f. fuscus* and *D. f. carolinensis*. They form a small but distinct dorsal protuberance at the base of the tail of the male *Eurycea multiplicata*. This glandular mass develops even in the male larva of the latter species before metamorphosis and is prob-

ably homologous with the less glandular tail-spine of *Salamandra caucasica*. The enlarged glands scattered over the head and body of the male *Typhlomolge* have been found to be hedonic glands. Usually the hedonic glands are not visible for the hypertrophied mass which forms the mental gland." Noble (1929, p. 4), states that he has found hedonic glands in male *Desmognathus phoca*, *D. f. fuscus*, *D. f. carolinensis*, *Leurognathus m. intermedia*, *Plethodon cinerus*, *P. jordani*, *Hydromantes italicus*, as well as in the species already mentioned. "Only in *Ancides lugubris* and *A. aeneus*," states Noble (1929, p. 5), "have apparently homologous glands been found in both sexes. These glands are widely spread over the lower sides of the body and ventral surfaces of both sexes and are readily visible in the living animal as yellowish spots."

All evidence to date seems to indicate that the hedonic glands are a secondary sexual character, and that actually the glands function only just before and during the breeding season. According to Noble (1931, p. 137), the secretions of the hedonic glands of newts and plethodontid salamanders have no recognizable odor to man and yet they seem to function in holding the attention of the female during courtship.

#### ORIGIN AND GENERAL CHARACTERISTICS OF THE HEDONIC GLAND-CLUSTER

As to the origin of the hedonic glands, Noble believes that they have apparently arisen from the mucous glands during phylogeny, and have developed into another type of gland of totally different function. "The male *Plethodontidae*," according to Noble (1931, p. 136), "develops glands having a slightly granular secretion which apparently serves to attract the female. A patch of these glands on the chin usually becomes enlarged to form a conspicuous pad."

It is not difficult to believe that the hedonic glands have arisen from the mucous glands which are found throughout the skin of the salamander, because of their close similarity in structure. There is, however, enough difference in the structure of the two types of glands to distinguish one from the other. In general, the cluster of mental hedonic glands consists of a mass of glands, each lined with secretory cells which produce a finely granular secretion. The individual glands are enveloped in a thin connective tissue membrane or network, while the cluster is limited internally by a relatively thicker layer of connective tissue, the limiting connective tissue membrane (hereafter referred to as the *limiting membrane*),

which appears to contain a few muscle cells. The cluster is limited externally by the epidermis, and the necks of the glands through which the secretions flow, are found protruding into the epidermis and open at its external surface.

There is no apparent physical mechanism which causes the secretions of the glands to flow. Probably, however, the glands of the plethodontoid salamanders are of the holocrine type, as Smith (1941, p. 259), has described them in *Triturus torosus*, and that during the breeding season, especially during courtship, the secretory cells burst or disintegrate when external pressure is applied to the glands and this causes the secretions to flow. Microscopic examination indicates that the few muscle cells present in the limiting membrane would be insufficient to force the secretions from the glands.

The mental hedonic glands show little or no microscopic variation throughout the family *Plethodontidae*. In general, the glands seem to be simply constructed, with the individual glands standing perpendicular to the epidermis, with their external pore openings at its surface. The secretory cells which are generally of the columnar type are arranged perpendicular to the walls of the glands. The nuclei of the secretory cells are elliptical to globular in shape, and when elliptical are found with their long axes parallel to that of the cells.

Macroscopic examination of the clusters of glands, however, shows some degree of variation in the different genera and species examined. These variations are evident as differences in size and shape of the clusters, the number of glands and their arrangement, and the presence or absence of pigmentation in the limiting membrane.

#### SEASONAL VARIATION

In general, the clusters of glands examined displayed a large degree of uniformity in development regardless of the time of year when the specimens were taken. In one species, however, a marked degree of seasonal variation was found in the cluster. Several specimens of *Bolitoglossa platydactyla* taken at Cuautlapan, Veracruz, in January, 1939, showed little or no evidence, either macroscopically or microscopically, of glands differing from the surrounding mucous glands. But specimens taken from the same location in July, 1940, displayed a prominent cluster of mental hedonic glands. One of the specimens taken in January was sectioned and the area in which the glands normally appear was covered with glands differing in no apparent manner from the mucous glands found in the rest of the

dermis of the salamander. Only a few of the specimens taken in January showed any evidence of differentiated hedonic glandular tissue. The undeveloped glands were short, and somewhat mushroom-shaped. Externally there was no elevation marking the presence of the cluster, but there was a slight differential coloration marking its location. This species of salamander was the only one that showed seasonal variation, but Smith (1941, p. 259), mentions that in *Triturus torosus*, "the greatest development of the hedonic glands is exhibited by *torosus* males in the height of breeding condition prior to amplexus." However, in the collection of Plethodontid salamanders studied, by far the largest part was collected in the months of June, July, August and September.

### GENERIC AND SPECIFIC CHARACTERISTICS OF THE GLANDS AND GLAND-CLUSTERS

#### GENUS PSEUDOEURYCEA Taylor

The mental hedonic gland-clusters vary in size and shape in this genus. They are circular in *Pseudoeurycea c. cephalica* and *P. belli*; broadly oval in *P. c. rubrimembris*; and they are almost triangular in *P. leprosa* and *P. gadovii*. In all the species examined the gland-clusters are composed of many glands which are generally not uniform in size and shape, *P. belli* being exceptional in having glands of relatively uniform diameter. The limiting membrane marking the dorsal boundary of the cluster is of approximately the same thickness as that found in the other genera. The granules of dark pigment found in this membrane, scattered at random between the bases of the glands, are missing only in *P. gadovii*.

In microscopic section the glands seem to be long and cylindrical, the dorsal end (base) being closed, while the ventral end (apex) is narrowed to a small tube, which terminates at the surface of the epidermis in a small external pore. The glands are all distinctly separated from each other by a thin layer of connective tissue, which envelops each of them, but they are, in general, closely approximated. The glands contain cells of the tall columnar type, containing a finely-granular cytoplasm, and a nucleus varying from globular to elliptical in shape. The bases of the cells rest upon the wall of the glands, and the long axes of the cells are perpendicular to the long axes of the glands. The nuclei are situated near the bases of the cells and when they are elliptical their long axes are parallel to that of the cells. There is a lumen present in the central part of the glands where the secretions from the cells presumably are collected before being ejected.

The regions between the narrowed necks of the glands contains small vacuoles of fat, masses of connective tissue, or small blood vessels. The limiting membrane, which marks the dorsal border of the cluster, is composed of short, thin fibers that cover the hedonic gland-cluster and extend away from it in all directions. The muscle cells are few in number, and are scattered throughout the walls of the glands, and occasionally in the limiting membrane. There is no distinct physical separation between the hedonic and mucous glands, but the differences in size and affinity for stain between these two types of glands are marked in the two species from which glands were sectioned.

In this genus the mental hedonic gland-clusters are easily recognized when the chin of the animal is observed. The cluster, in all species, is evident as an area lighter in color than that of the surrounding skin, and in this genus the cluster presents an elevation along its posterior and lateral borders in all the species examined except *P. gadovii* in which the elevation is most prominent in the center of the cluster. The gland-clusters in the species of this genus when intact, lie flat in a shallow cavity formed in the musculature of the lower jaw.

Microscopic sections of the gland-cluster of *P. leprosa* show that the individual glands are closely crowded together and that they are wrinkled and distorted. This wrinkling is probably the result of either degeneration or internal compression within the cluster. The thin envelope of connective tissue surrounding each gland is also wrinkled and this made identification of the individual glands somewhat difficult. Although the gland-cluster of only one specimen was sectioned, macroscopic examination of the clusters in numerous other specimens indicated that this wrinkled condition was common to all of them.

The glands of the cluster in *P. c. rubrimembris*, are irregular in diameter, some being six to eight times larger in diameter than others, while in the other species the glands are relatively uniform in diameter within each species.

The gland-clusters in this genus resemble some of those in the other genera examined. A description of the physical characteristics of the gland-clusters of the *Pseudoeurycea* are presented in Table I, and from this as well as the text and drawings resemblances between the clusters of the species of this genus and others can be seen. The macroscopic physical characters are sufficient for identification of each species examined.



There is no physical separation between the hedonic and mucous glands. The shape of the two types of glands and their individual affinities for stain are sufficient characters to differentiate them, as is seen in the drawings in Plate I (fig. 7).

#### GENUS CHIROPTEROTRITON Taylor

The species of this genus are generally of medium size as compared to the other genera examined in this investigation. The shape of the hedonic gland-clusters in this genus varies greatly; some are subtriangular, some are subcircular, and others are ovoid. The gland-clusters are made up of a single layer of glands, limited internally by the limiting membrane which is uniformly thin throughout the genus. The glands are relatively large, and in general, are less numerous than in the other genera except *Thorius* and *Oedipina*. *Chiropterotriton lauae* is an exception having a large number of glands. The cells line the walls of the glands and the axes of the elliptical nuclei are parallel to those of the cells. The cells are mostly of the tall columnar type and stain similarly to those of the surrounding dermal layer. The glands are generally "cone-shaped," and are each distinctly enveloped in a membrane or network of connective tissue. In most species the glands seem to be separated from each other more than they are in the other genera, giving the cluster an appearance of being loosely constructed.

Any difficulty encountered in discerning externally the gland-clusters of the species in this genus is usually because they are so small, and the elevation produced by the presence of the cluster is easily overlooked; however, in all species there is some difference in the color of the epidermis covering the cluster from that of the surrounding area.

Microscopic sections of the gland-clusters of the species in this genus show essentially the same structure as that seen in the species of *Pseudoeurycea*. The same relationship is noted between the position of the cells and cell nuclei to the gland walls. The nuclei of the cells, when elliptical, are parallel to the axis of the cells, as in *Pseudoeurycea*.

The specimen of *C. chiroptera* selected for microscopic examination seems to have been taken in the breeding season, since the cells of the glands were greatly swollen and contained a heavy granular material. Some of the cells appeared so heavily laden with this material that their walls had either burst, or were destroyed in fixation, because the granular material had been released into the lumina of the glands. The cells, which were distinguishable in the sections,

had shifted their position and instead of being perpendicular to the axis of the glands appeared to be directed toward the external pores. The nuclei, which stain very deeply, lie almost flat against the wall of the gland, and also seemed to be directed toward the external pores. The granules in the cells and in the lumina of the glands stained a bright golden color with Mallory's triple stain.

The gland-clusters of several specimens of *C. dimidiata* examined exhibited a slight protuberance at the extreme posterior median border. This protuberance, as can be seen in Plate II, fig. 5, is caused by the considerable enlargement of a single gland which is about 1.5 times larger than any of the others in the cluster.

The gland-cluster of *C. arborea* exhibited a characteristic structure. Observation of the dorsal surface of the cluster showed a trilobate condition, being caused by an elongation of the glands in the median anterior-posterior region. The glands in the lateral regions, being shorter, accentuate this trilobate appearance of the cluster. The cavity in the musculature of the lower jaw presents a similar appearance, the median anterior and posterior part being markedly deeper than the lateral parts. Microscopic sections of this cluster show essentially the same structure as that seen in *C. chiroptera*. The sections of *C. arborea* also show greatly swollen glands containing a heavy granular material. The granules are the same bright golden color and are of the same approximate size as those seen in *C. chiroptera*. In the glands of *C. arborea*, however, the majority of the columnar cells have their long axes perpendicular to the walls of the glands, and the nuclei are globular rather than elliptical as in *C. chiroptera*.

The gland-clusters in this genus, as in the *Pseudoeurycea*, lie in a shallow cavity in the musculature of the lower jaw when intact. The physical characters of the clusters of the species of *Chiroptero-triton* examined are presented in Table II.

#### GENUS LINEOTRITON Tanner

One species of the genus *Lineotriton* (*L. lineola*) was available for investigation. A description of the physical characteristics is presented in Table III, and a drawing of the gland-cluster is found in Plate III, fig. 1. On the basis of this one species the cluster is seen to be similar in structure to those of the other genera except *Thorius* and *Oedipina*.

GENUS *BOLITOGLOSSA* Duméril and Bibron

The species of the genus *Bolitoglossa* are considerably larger than those of the genera previously discussed. In general, the gland-clusters of this genus are subcircular to somewhat cordiform, with the apex directed anteriorly, and one species displays a curious asymmetry. The individual glands are small and numerous, and in all the species but *B. schmidti* they are distinctly separated from each other. They are, in general, uniform in size and number within a given species, but there is much contrast between different species, while the whole clusters may be of similar proportions. Also characteristic of the various species is the presence of numerous granules of dark pigment in the limiting membrane, scattered between the bases of the glands.

Microscopically the clusters appear to be constructed simply with the glands situated side by side, as may be seen in the drawing of a section of the cluster of *B. mexicana* (Plate III, fig. 9). The relationship between cell nuclei, cells, and glands is the same in this genus as in *Pseudoeurycea*. Microscopic sections, moreover, show that the structures of the clusters in this genus resemble those of the *Pseudoeurycea* in every respect except size.

The gland-cluster of *B. platydactyla* is characterized by a protuberance at its posterior median border. In all of the specimens studied of this species, the gland-cluster displayed a curious asymmetry, having one side rounded, and the other flattened. The drawing (Plate III, fig. 3) illustrates one of the more extreme examples of this asymmetry.

The gland-clusters of *B. rufescens* are also distinctively shaped. In the specimens examined they are somewhat cordiform, but the lateral borders in the anterior part of the cluster are concave. In all of the other species examined in this investigation the lateral borders are convex. Another characteristic of the cluster of this species is the arrangement of the dark granules of pigment found in the limiting membrane. The granules in the cluster of *B. rufescens* tend to segregate along the midline, forming a dark band. There are, however, numerous other granules scattered at random throughout the rest of the limiting membrane.

The gland-clusters in the species of this genus, as in the previously described genera, when intact, lie in a shallow cavity in the musculature of the lower jaw. The physical characters of the gland-clusters in the species examined of the genera *Lineotriton* and *Bolitoglossa* are presented in Table III.

GENUS *MAGNADIGITA* Taylor

The gland-clusters in the genus *Magnadigita* are variable in shape, but relatively uniform in size. They are circular, somewhat triangular, or oval in the different species. They are characteristically thin and composed of many glands that are uniform in shape. In this genus, as in *Bolitoglossa*, there are dark granules of pigment in the limiting membrane situated between the bases of the glands. The limiting membrane is somewhat thicker than in the genus *Chiropterotriton*, and resembles that in *Bolitoglossa*.

Microscopically the epidermis covering the clusters in this genus is thicker than that in either *Chiropterotriton* or *Bolitoglossa*, but aside from this difference, the structure of the clusters is similar to that of the other genera, and in gross examination without the aid of a dissecting microscope, and without a count of the glands in each cluster, it would be difficult to differentiate them. There are, however, enough variations in numbers of glands in each cluster to distinguish the genera.

Microscopic sections of the gland-clusters of *M. nigroflavescens*, (Plate IV, fig. 6), shows the close relationship between the hedonic and mucous glands. There is no sharp line of separation between the two. The limiting membrane does not separate the two types of glands but seems to hold them together. The membrane, however, is not so thick over the mucous glands as it is over the hedonic glands. The mucous glands are much smaller and are more or less balloon-shaped, and their nuclei do not stain as intensely as do those of the hedonic glands. The mucous secretions stain blue rather than golden with Mallory's triple stain.

A view of the dorsal surface of the gland-cluster of *M. subpalmata* (Plate IV, fig. 4), shows a somewhat different structure than is seen in the clusters of the other species. The glands in the anterior part of the cluster of *M. subpalmata* are widely separated from each other. This separation of the glands is characteristic of all the specimens studied. The separations in the other parts of the cluster, however, are irregular.

The physical characteristics of the gland-clusters of the species investigated in this genus are given in Table IV, and drawings of the clusters are in Plate IV. As in the other genera and species discussed, the gland-clusters when intact, lie in a shallow cavity in the musculature of the lower jaw.

## GENUS THORIUS Cope

This Mexican genus of small salamanders is characterized by gland-clusters which are large in relation to the size of the animal, and are generally circular and flat. The number of glands per cluster varies greatly among the various species examined, but is relatively constant within each species. In general, the glands are more widely separated in all species than in the other genera. The cluster, when intact, lies flat in a shallow cavity in the musculature of the lower jaw, and is marked externally by a slight differential coloration of the skin covering the cluster, and in all species, except *Thorius* sp. (#29528, EHT-HMS), a slight elevation is present at the posterior border. The only microscopic differences detected in the structure of the gland-clusters of this genus and the others, were that the cluster is smaller, and that the glands are shorter and smaller in diameter than in the previously described genera. The relationship between cell nuclei, cells, and their position in the glands are the same as described for the other genera, as can be seen in Plate V, figure 8. The dermal layer and the limiting membrane while thinner than in the other genera, make up almost half of the thickness of the gland-cluster, and the dark granules found in the limiting membrane of some other genera are lacking in this genus, as in the gland-clusters of *Chiropterotriton*.

A view of the dorsal surface of the clusters of *T. macdougalli* and *T. pennatulus*, shows that the glands are irregular in size, the largest being up to ten times the size of the smallest. Also the glands are irregular in shape, being circular to broadly oval in cross-section. The same surface of *Thorius* sp. (a small undescribed form characterized by a small nostril), shows a corresponding irregularity in size among the glands, the largest being six to eight times the size of the smallest, and varying between circular and broadly oval in cross-sectional shape. Some of the glands in the clusters of *T. dubitus* are five to six times larger than others, and they vary in shape from circular to oval.

The physical characteristics of the gland-clusters of this genus are given in Table V, and drawings of the clusters are in Plate V.

## GENUS OEDIPINA Keferstein

The hedonic gland-clusters of the genus *Oedipina* differ markedly from those of the other genera investigated. The individual glands and their basic constituents are essentially the same as those in the other genera, but the glands, originating in a small area in the sub-

mandibular region, are long, slender tubules lying horizontally between the musculature of the lower jaw and the skin. They extend for a number of millimeters posteriorly in a fanlike manner. The number and length of the glands varies with each species, but the cluster in each is typically fan-shaped, with occasional specimens having the glands overlapping. The external pores are close together. The glands which connect with the more anterior pore openings are situated dorsal to the glands connecting with the more posterior pores.

The limiting membrane also differs in this genus. The glands have seemingly pushed almost through this membrane and seem to be nearly in contact with the muscular layers in the lower jaw; however, the glands are seen in microscopic section to be surrounded by a thin network of fibers similar to those found in the limiting membrane which separates them from the musculature. With the exception of being more elongate, the glands are similar in microscopic structure to those found in the other genera. The cells are arranged around the periphery of the glands with their long axes perpendicular to the long axes of the glands. The cell nuclei are elliptical to globular in shape and are situated at the bases of the cells, oriented so that their long axes are parallel to the long axes of the cells. Microscopic sections also show that the mucous glands are somewhat suppressed in the area immediately surrounding the external pores.

The gland-clusters in this genus are not easily observed because there is only a slight external elevation, and the color of the epidermis covering the clusters differs but little from that of the surrounding skin. The cluster is placed well forward, just posterior to the symphysis of the mentomeckelian bones.

No microscopic sections were made of the clusters of *O. uniformis* and *O. bonitaensis*. Probably, however, the structure is similar to that of *O. Cyclocauda*, since they resemble each other in macroscopic structure. The minor differences in structure make identification of the gland-clusters of this genus easy, both macroscopically and microscopically. Descriptions of the physical characteristics of the gland-clusters of the species of *Oedipina* investigated are in Table VI, and drawings of the individual clusters are found in Plate VI.

SPECIFIC AND GENERIC RELATIONSHIPS AS  
INDICATED BY THE STRUCTURE OF THE GLAND-CLUSTERS

It is evident from the preceding material that there is a definite resemblance in position, size and shape of the mental hedonic gland-clusters of the various species and genera investigated. It is doubtful that one could differentiate the cluster of any given species or even genus from microscopic sections alone; the exception, of course, being *Oedipina*. The similarity mentioned is interesting, but not surprising when one considers that there is a corresponding similarity between many of the homologous structures in the genera of almost every taxonomic family in the Animal Kingdom.

There are enough macroscopic variations among the different genera and species for one to be able to establish some relationships between them. Of the variations of a major type, the most evident is the elongation and recumbent position of the glands in the gland-clusters of the genus *Oedipina*. The fact that the glands in the clusters of *Oedipina* have been able to penetrate into and almost through the limiting membrane is significant, because this character has not been developed in the clusters of the other genera. The gland-clusters in *Oedipina* are, therefore, considered highly specialized.

The other species and genera examined show little variation in the degree of development. The clusters of the species of *Pseudoeurycea* seem to be the most generalized of those examined, in that there is little differentiation in the size and shape of the clusters, and the individual glands are only slightly varied, in number, size and shape. In the genera *Magnadigita*, *Bolitoglossa* and *Chiropoterotriton* the clusters, as well as the individual glands are more variable in size and shape, and thus seem somewhat more highly differentiated. The genus *Lineotriton* probably also belongs with this latter group.

The larger species of the genus *Bolitoglossa* have larger gland-clusters composed of more numerous glands than the smaller species; while in *Magnadigita* and *Pseudoeurycea* the larger species (*M. robusta* and *P. bellii*) have smaller clusters containing fewer glands than do the medium sized species of these genera.

There is a remarkable similarity between the gland-clusters of *Magnadigita pesrubra*, *Bolitoglossa mexicana*, *B. schmidti* and *Pseudoeurycea c. cephalica*. There are minor differences but the cluster of *P. c. cephalica* is the most obviously different in that it contains fewer glands. The clusters of *Bolitoglossa mexicana* and

*B. schmidti* differ somewhat in size, but both have approximately the same number of glands, and the glands of both species are irregular in size and shape. The cluster of *Magnadigita pesrubra* also has the same dimensions, as well as an equal number of glands, but differs from the others in that the glands are notably uniform in size and shape.

The gland-clusters of the subspecies *Pseudoeurycea c. cephalica* and *P. c. rubrimembris* differed markedly in shape and number of glands, those of the latter being an elongate oval and containing more glands. The relationship of the individual glands within each cluster, however, is similar in that in both they are non-uniform in size and shape, and are closely approximated.

The gland-clusters found in *Bolitoglossa rufescens* differ from those of the rest of the genus. The animal is small but has a relatively small cluster. The shape is somewhat similar to that in *B. striatula* and *B. veracrucis*, but differs markedly from the rest. It is less than half as large proportionally as any other cluster seen in the genus, and contains by far the smallest number of glands. The individual glands are similar to those seen in *B. platydactyla*, *B. mexicana*, and *B. schmidti* only in that they are non-uniform in size and shape, and showed the same microscopic morphology.

If the species of the genus *Chiropterotriton* are divided as to habitat, it is noticed that the arboreal forms (*C. arborea* and *C. lavae*) have a cluster similar in size and shape to the terrestrial forms, but containing two to three times more glands. The cluster of *C. multidentata*, which is found in both habitats, is intermediate between the arboreal and terrestrial forms in number of glands, having more than the terrestrial species and less than the arboreal species. Of the terrestrial forms, however, *C. chondrostega* which has never been taken from bromelias, but has been found only under rocks in open terrain, has almost the same number of glands as the arboreal species. The number of its glands suggests that it is either related in some manner to the arboreal forms, or that it is a somewhat aberrant terrestrial form. The number of glands may in some manner be associated with habit and habitat.

In the genus *Thorius*, *T. dubitus*, *T. macdougalli*, *Thorius sp.*, and *T. pennatululus* show considerable variation in the relative size and shape of the individual glands. In the other species of this genus, however, the gland-clusters varied but little from those in the genera *Magnadigita*, *Bolitoglossa* and *Chiropterotriton*, except that, owing to the much smaller size of the animals, the clusters were smaller.



If the external pressure applied to the glands during courtship is the stimulus required to cause secretion, it would be of interest to know what effect pressure would have on a gland of the type found in *Oedipina*. It is not known whether the chin of the male is moved from side to side, or from anterior to posterior during courtship. If the latter type of movement is utilized the secretions probably would be thrust forward and then expelled. If, on the other hand, the movement is lateral, it would seem difficult for the secretions to be forced out of the glands.

#### SUMMARY

1. In the family *Plethodontidae*, the mental hedonic gland-cluster is embedded in the skin immediately posterior to the symphysis of the mentomeckelian bones in the submandibular region of the males.
2. Macroscopic and microscopic examination showed that the gland-clusters of the genus *Oedipina* are the most specialized in size, shape and development.
3. The gland-clusters of the other genera show varying degrees of specialization; the clusters of *Pseudoeurycea* are the most generalized and those of *Chiropterotriton*, *Bolitoglossa*, and *Magnadigita* are somewhat more specialized. The clusters seen in the genus *Thorius* stand somewhere between those of *Oedipina* and those of other genera. The cluster of only one specimen of *Lineotriton lineola* was available for investigation, however, it also appears to belong in this group.
4. There are certain intergeneric, interspecific and intraspecific relationships in the clusters of the various genera and species which may depend on habitat, breeding habits, and other factors not fully considered in this investigation.
5. In all the species examined within a given genus, the clusters of *Bolitoglossa rufescens* seem to be the most aberrant in form.

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TABLE I  
 PHYSICAL CHARACTERISTICS OF THE GLAND-CLUSTERS OF THE GENUS *PSEUDOEURYCEA*

	<i>P. c. cephalica</i>	<i>P. leprosa</i>	<i>P. gadovii</i>	<i>P. c. rubrimembris</i>	<i>P. belti</i>
Length of cluster * . . . . .	2.5	2.8	3.0	2.2	2.4
Width of cluster . . . . .	2.5	3.0	4.0	3.2	3.0
Thickness of cluster . . . . .	0.6	0.8	1.0	0.5	0.5
Shape of cluster . . . . .	Circular.	Triangular; rounded posteriorly, blunt apex anterior.	Triangular; flattened posteriorly, blunt apex anterior.	Broadly oval.	Ovoid to circular.
Number of glands . . . . .	130	275	110	198	140
Length of glands . . . . .	0.57	Too distorted to measure.	Uniform (macroscopically)	Uniform (macroscopically)	0.39
Diameter of glands . . . . .	0.08—0.19	Too distorted to measure.	Uniform (macroscopically)	Some 6—8 times larger than others.	0.16
Thickness of limiting membrane . . . . .	0.02	0.028	Thinner than <i>P. leprosa</i> .	Approximately same as <i>P. c. cephalica</i> .	0.03
Granules of pigment . . . . .	5—7, dark and irregularly shaped.	Occasional group in posterior portion.	None.	Numerous, scattered at random.	Numerous, scattered at random.
Remarks . . . . .	Individual glands distinctly separated. Granules of pigment segregated to areas between bases of glands.	Granules of pigment seem to be restricted to posterior part of cluster.	No microscopic sections made.	No microscopic sections made. Individual glands are separated in center of cluster; closely approximated around periphery.	

\* All measurements in mm.

TABLE II  
 PHYSICAL CHARACTERISTICS OF THE GLAND-CLUSTERS OF THE GENUS *CHIROPTEROTRITON*

	<i>C. multidentata</i>	<i>C. terrestris</i>	<i>C. chiropptera</i>	<i>C. larvae</i>	<i>C. dimidiata</i>	<i>C. chondrostegia</i>	<i>C. arborea</i>
Length of cluster.....	1.0	1.0	1.0	1.0	1.1	0.8	1.5
Width of cluster.....	2.0	1.5	1.5	1.5	1.0	1.0	2.0
Thickness of cluster.....	0.4	0.5	0.6	0.6	0.6	0.4	0.8
Shape of cluster.....	Ovoid, lateral borders broadly rounded.	Ovoid.	Triangular; base broadly rounded, blunt apex directed anteriorly.	Triangular; shape more sharply angular than <i>C. chiropptera</i> .	Broadly oval, bluntly pointed anteriorly.	Ovoid.	Broadly oval.
Number of glands.....	75-80	48-50	50-52	170-175	60	160-170	205-207
Length of glands.....	0.2	0.33	0.5	0.33	Circular to almost rectangular in cross-section.	0.21	0.7
Diameter of glands.....	0.18	0.13	0.1	0.12	Approximately same thickness as <i>C. larvae</i> .	0.16	0.16
Thickness of limiting membrane.....	0.02	0.02	0.02	0.02	0.03	0.03	0.02
Granules of pigment.....	None	None	None	None	None	None	None
External elevation of cluster...	Marked, along lateral and posterior borders.	Slight, along posterior border.	Slight, along posterior border.	Center of cluster elevated more than posterior border.	Slight, along posterior border.	Rounded with peak at center.	Slight elevation along posterior border.
External coloration of cluster...	Lighter than surrounding area.	Lighter than surrounding area.	Slightly lighter than surrounding area.	Markedly lighter than surrounding area.	Slightly lighter than surrounding area.	Slightly lighter than surrounding area.	Slightly lighter than surrounding area.
Remarks.....	Bases of glands circular to almost rectangular in cross-section. Glands separated in some areas, closely approximated in others.	Glands distinctly separated from each other.	Glands in center of cluster are distinctly separated from each other.		No microscopic sections made.	Glands closely approximated.	Trioblate appearance of cluster.

TABLE III  
PHYSICAL CHARACTERISTICS OF THE GLAND-CLUSTERS OF THE GENERA *LINEOTRITON* AND *BOLITOGLOSSA*

	<i>I. tinea</i>	<i>B. mexicana</i>	<i>B. platydaetula</i>	<i>B. striatula</i>	<i>B. flaviventris</i>	<i>B. veracrucis</i>	<i>B. rufescens</i>	<i>B. schmidti</i>
Length of cluster...	1.2	3.2	5.2	4.5	4.0	2.9	1.5	2.6
Width of cluster...	1.2	3.2	5.9	4.8	4.0	4.0	1.8	2.8
Thickness of cluster...	0.3	1.0	0.6	0.5	0.2	0.4	0.2	0.8
Shape of cluster...	Circular.	Circular.	Ovoid; see text.	Cordiform; apex directed anteriorly.	Cordiform; apex directed anteriorly.	Cordiform; broadened laterally.	Cordiform; lateral borders in anterior part concave.	Circular.
Number of glands...	198	225—235	330—340	500	400	400	150—160	200
Length of glands...		0.66			Relatively short.	Longer than in <i>B. flaviventris</i> .	0.16	
Diameter of glands...	Oval in cross-section.	0.22	Nonuniform in diameter.	Uniform in diameter.	Uniform in diameter.	Nonuniform in diameter.	0.10	Nonuniform in diameter.
Thickness of limiting membrane		0.2	Approximately the same as <i>B. mexicana</i> .	Thicker than <i>B. mexicana</i> .	None.	5—8 granules segregated in anterior part.	0.05	Thinner than in <i>B. rufescens</i> .
Granules of pigment	Occasional clusters scattered at random.	Numerous, segregated to median anterior third of cluster.	Numerous, scattered at random.	Numerous, scattered in anterior part.	None.	Marked, along posterior border.	Form dark anterior-posterior band along mid-line.	Occasional, scattered at random.
External elevation of cluster	Along lateral and posterior borders.	Marked, along posterior border.	Entire surface of cluster elevated.	None.	Slight, along posterior border.	Marked, along posterior border.	None.	Marked, along posterior border.
External coloration of cluster	Slightly lighter than surrounding area.	Lighter than surrounding area.	Markedly lighter than surrounding area.	Slightly lighter than surrounding area.	None; color of cluster same as venter of animal.	Lighter than surrounding area.	None; color of cluster same as venter of animal.	None; color of cluster same as that of venter of animal.
Remarks....	No microscopic sections made.	No microscopic sections made. Cluster had definite yellowish color. Individual glands widely separated.	No microscopic sections made. Individual glands relatively small and closely approximated.	No microscopic sections made. Glands closely approximated.	No microscopic sections made. Glands closely approximated.	No microscopic sections made.	None.	No microscopic sections made. Glands closely approximated.

TABLE IV  
 PHYSICAL CHARACTERISTICS OF THE GLAND-CLUSTERS OF THE GENUS *MAGNADIGITA*

	<i>M. torresi</i>	<i>M. pesrubra</i>	<i>M. nigroflavescens</i>	<i>M. subpalmata</i>	<i>M. robusta</i>
Length of cluster.....	2.5	2.5	2.5	2.8	4.5
Width of cluster.....	2.5	3.0	2.6	3.3	3.5
Thickness of cluster....	0.4	0.4	0.3	1.1	0.9
Shape of cluster.....	Circular.	Circular, flattened along posterior border.	Circular.	Somewhat cordiform; bluntly pointed anteriorly; posteriorly, border slightly concave.	Elongate oval; bluntly pointed anteriorly; posteriorly broadly rounded.
Number of glands.....	250	200	180-185	195-200	180
Length of glands.....			0.25	1.0	Shorter than <i>M. subpalmata</i> .
Diameter of glands....	Uniform in diameter.	Uniform in diameter.	0.18	0.19	Nonuniform in diameter.
Thickness of limiting membrane..	Relatively thick.	Approximately the same as <i>M. torresi</i> .	0.01	0.01	Appears thicker than in <i>M. subpalmata</i> .
Granules of pigment....	Numerous, scattered at random.	8-10 granules along antero-posterior mid-line.	15-18 granules scattered at random.	Occasional, scattered at random.	Occasional cluster of granules scattered at random.
External elevation of cluster.....	Marked, along posterior border.	Slight, along posterior border.	None.	Marked, along posterior border.	Whole cluster strongly elevated.
External coloration of cluster.....	Markedly lighter than surrounding area.	Markedly lighter than surrounding area.	Slightly lighter than surrounding area.	Markedly lighter than surrounding area.	Markedly lighter than surrounding area.
Remarks.....	No microscopic sections made. Glands closely approximated.	No microscopic sections made.		Glands in anterior part separated. Granules of pigment not restricted to areas between bases of individual glands.	No microscopic sections made. Glands around periphery smaller in diameter and closely approximated, those in center larger in diameter and widely separated.

TABLE V  
PHYSICAL CHARACTERISTICS OF THE GLAND-CLUSTERS OF THE GENUS *THORIS*

	<i>T. narisovatis</i>	<i>T. pulmonaris</i>	<i>T. macdougalli</i>	<i>Thoris</i> sp.	<i>T. pennatulus</i>	<i>T. dubitus</i>	<i>T. troglodytes</i>
Length of cluster.....	1.0	0.8	0.8	0.8	0.8	0.8	1.1
Width of cluster.....	1.1	0.9	0.8	0.8	0.8	0.7	0.8
Thickness of cluster.....	0.3	0.2	0.2	0.2	0.2	0.2	0.3
Shape of cluster.....	Circular.	Circular.	Circular.	Circular.	Circular.	Elongate oval.	Somewhat cordiform, bluntly pointed posteriorly.
Number of glands.....	99	140	50	42	17	64	70
Length of glands.....	0.16	Shorter than <i>T. narisovatis</i> .					
Diameter of glands.....	0.1	Uniform in diameter.	Nonuniform.	Nonuniform.	Nonuniform.	Nonuniform.	Uniform.
Thickness of limiting membrane	0.015	Approximately the same as <i>T. narisovatis</i> .	Seems thicker than <i>T. narisovatis</i> .	Approximately the same as <i>T. narisovatis</i> .	Thicker than <i>T. narisovatis</i> .	Approximately the same as <i>T. narisovatis</i> .	Thicker than <i>T. narisovatis</i> .
Remarks.....		No microscopic sections made.	No microscopic sections made. Glands distinctly separated.	No microscopic sections made.	No microscopic sections made.	No microscopic sections made. Glands closely approximated.	No microscopic sections made. Glands closely approximated.

TABLE VI  
 PHYSICAL CHARACTERISTICS OF THE GLAND-CLUSTERS  
 OF THE GENUS *OEDIPINA*

	<i>O. cyclocauda</i>	<i>O. uniformis</i>	<i>O. bonitaensis</i>
Position of external pores..	In two irregular rows near the tip of the chin	In two distinct rows near the tip of the chin.	Form three or possibly four rows, appear somewhat as a circular group.
Shape of cluster.....	Fan-shaped.	Fan-shaped.	Fan-shaped.
Number of glands.....	9	11	17
Length of glands.....	1.4	1.2—1.4	1.5—1.8
Diameter of glands.....	0.08	Approximately the same as <i>O. cyclocauda</i> .	Approximately the same as <i>O. cyclocauda</i> .
Thickness of limiting membrane.....	0.04 thickening to 0.1 around apices of glands.	Approximately the same as <i>O. cyclocauda</i> .	Approximately the same as <i>O. cyclocauda</i> .
Remarks.....		No microscopic sections made.	No microscopic sections made. Diagrammatic sketch (Pl. VI, fig. 4.)



TABLE VII  
TABULATION OF CLUSTER SIZE AND GLAND NUMBERS

Genus and species	Length in mm.	Width in mm.	Thickness in mm.	Number of glands	Snout to vent in mm.
<i>Pseudoeurycea</i>					
<i>c. cephalica</i> .....	2.5	2.5	0.6	130	44.0
<i>leprosa</i> .....	2.8	3.0	0.8	275	48.0
<i>gadowii</i> .....	3.0	4.0	1.0	110	37.0
<i>c. rubrimembris</i> .....	2.2	3.2	0.5	198	43.0
<i>bellii</i> .....	2.4	3.0	0.6	140	93.0
<i>Chiropterotriton</i>					
<i>multidentata</i> .....	1.0	2.0	0.4	75—80	38.0
<i>terrestris</i> .....	1.0	1.5	0.5	48—50	26.5
<i>chiroptera</i> .....	1.0	1.5	0.5	50—52	25.0
<i>lavae</i> .....	1.0	1.5	0.6	170—175	33.0
<i>dimidiata</i> .....	1.1	1.0	0.6	60	24.7
<i>chondrostege</i> .....	0.8	1.0	0.4	160—170	29.0
<i>arborea</i> .....	1.5	2.0	0.8	205—207	34.8
<i>Lineotriton</i>					
<i>lineola</i> .....	1.2	1.2	0.3	198	34.5
<i>Bolitoglossa</i>					
<i>mexicana</i> .....	3.2	3.2	1.0	225—235	68.0
<i>platydactyla</i> .....	5.2	5.9	0.6	330—340	70.0
<i>striatula</i> .....	4.8	4.5	0.5	500	47.0
<i>flaviventris</i> .....	4.0	4.0	0.2	400	66.0
<i>veracruzis</i> .....	2.9	4.0	0.4	400	50.0
<i>rufescens</i> .....	1.5	1.8	0.2	150—160	31.0
<i>schmidti</i> .....	2.6	2.8	0.8	200	54.0
<i>Magnadigita</i>					
<i>torresi</i> .....	2.5	2.5	0.4	250	51.0
<i>pesrubra</i> .....	2.5	3.0	0.4	200	63.0
<i>nigroflavescens</i> .....	2.5	2.6	0.3	180—185	55.0
<i>subpalmata</i> .....	2.7	3.2	1.1	195—200	68.0
<i>robusta</i> .....	4.5	3.5	0.9	180	80.0
<i>Thorius</i>					
<i>narisovalis</i> .....	1.0	1.1	0.3	99	31.0
<i>pulmonaris</i> .....	0.8	0.9	0.2	140	27.2
<i>macdougalli</i> .....	0.8	0.8	0.2	50	20.7
<i>Thorius sp.</i> .....	0.8	0.8	0.2	42	.....
<i>pennatulus</i> .....	0.8	0.8	0.2	17	21.2
<i>dubitus</i> .....	0.8	0.7	0.2	64	21.0
<i>troglydytes</i> .....	1.0	0.8	0.3	70	26.0
<i>Oedipina</i>					
<i>cyclocauda</i> .....	1.4	0.08 mm.	diameter	9	43.0
<i>uniformis</i> .....	1.2—1.4			11	51.0
<i>bonitaensis</i> .....	1.5—1.8			17	56.0

## PLATE I

The Mental Hedonic Gland-clusters of the Genus *Pseudoeurycea*

FIG. 1. *Pseudoeurycea cephalica cephalica*. View of dorsal surface of gland-cluster,  $\times 12$ .

FIG. 2. *Pseudoeurycea leprosa*. View of dorsal surface of gland-cluster,  $\times 9$ .

FIG. 3. *Pseudoeurycea gadovii*. View of dorsal surface of gland-cluster,  $\times 6$ .

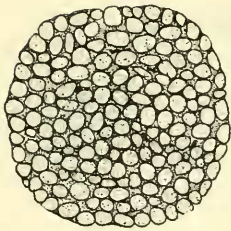
FIG. 4. *Pseudoeurycea cephalica rubrimembris*. View of dorsal surface of gland-cluster,  $\times 10$ .

FIG. 5. *Pseudoeurycea bellii*. View of dorsal surface of gland-cluster,  $\times 12$ .

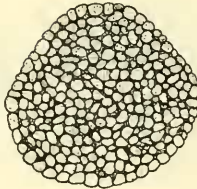
FIG. 6. *Pseudoeurycea leprosa*. Longitudinal cross-section,  $\times 48$ .

FIG. 7. *Pseudoeurycea bellii*. Longitudinal cross-section,  $\times 23$ .

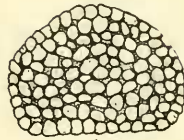
PLATE I



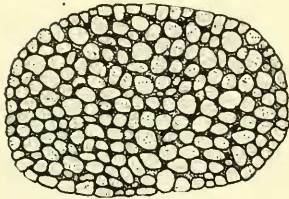
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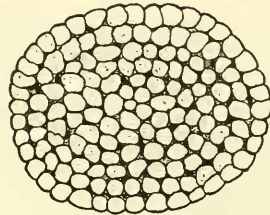
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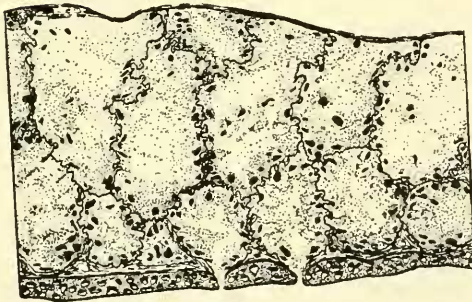
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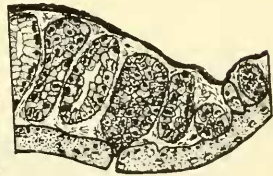
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## PLATE II

The Mental Hedonic Gland-clusters of the Genus *Chiropterotriton*

FIG. 1. *Chiropterotriton multidentata*. View of dorsal surface of gland-cluster,  $\times 18$ .

FIG. 2. *Chiropterotriton terrestris*. View of dorsal surface of gland-cluster,  $\times 19$ .

FIG. 3. *Chiropterotriton chiroptera*. View of dorsal surface of gland-cluster,  $\times 19$ .

FIG. 4. *Chiropterotriton laeae*. View of dorsal surface of gland-cluster,  $\times 19$ .

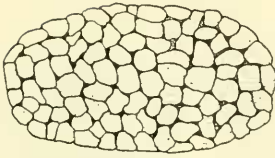
FIG. 5. *Chiropterotriton dimidiata*. View of dorsal surface of gland-cluster,  $\times 19$ .

FIG. 6. *Chiropterotriton chondrostega*. View of dorsal surface of gland-cluster,  $\times 19$ .

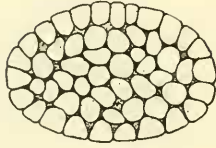
FIG. 7. *Chiropterotriton arborea*. View of dorsal surface of gland-cluster,  $\times 19$ .

FIG. 8. *Chiropterotriton chiroptera*. Longitudinal cross-section,  $\times 28$ .

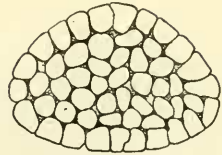
PLATE II



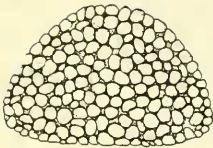
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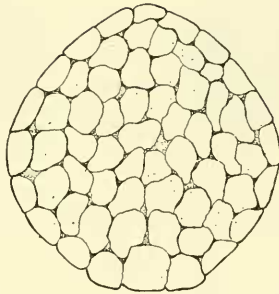
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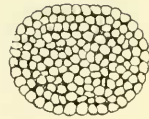
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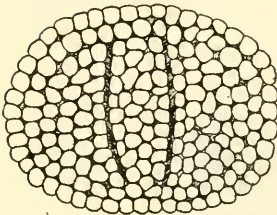
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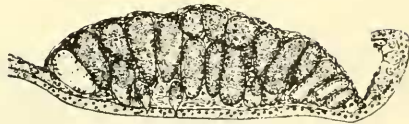
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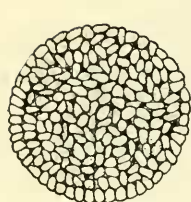
8.

## PLATE III

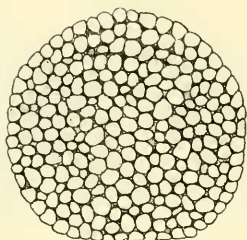
The Mental Hedonic Gland-clusters of the Genera *Lineotriton* and *Bolitoglossa*

- FIG. 1. *Lineotriton lineola*. View of dorsal surface of gland-cluster,  $\times 20$ .  
FIG. 2. *Bolitoglossa mexicana*. View of dorsal surface of gland-cluster,  $\times 10$ .  
FIG. 3. *Bolitoglossa platydactyla*. View of dorsal surface of gland-cluster,  
 $\times 5$ .  
FIG. 4. *Bolitoglossa striatula*. View of dorsal surface of gland-cluster,  $\times 7$ .  
FIG. 5. *Bolitoglossa flaviventris*. View of dorsal surface of gland-cluster,  $\times 5$ .  
FIG. 6. *Bolitoglossa veracrucis*. View of dorsal surface of gland-cluster,  
 $\times 10$ .  
FIG. 7. *Bolitoglossa rufescens*. View of dorsal surface of gland-cluster,  $\times 11$ .  
FIG. 8. *Bolitoglossa schmidti*. View of dorsal surface of gland-cluster,  $\times 10$ .  
FIG. 9. *Bolitoglossa mexicana*. Longitudinal cross-section of gland-cluster,  
 $\times 31$ .

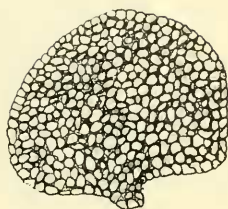
PLATE III



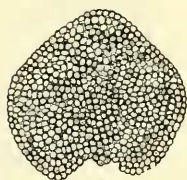
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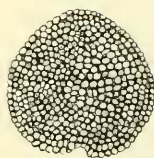
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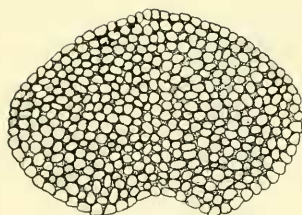
3.



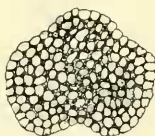
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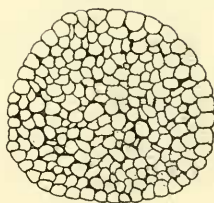
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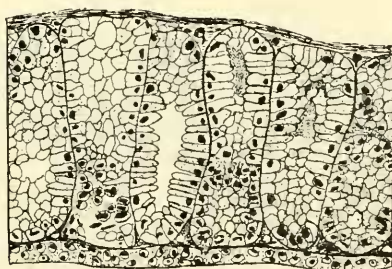
6.



7.



8.



9.

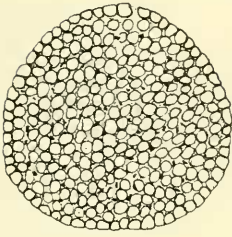
## PLATE IV

The Mental Hedonic Gland-clusters of the Genus *Magnadigita*

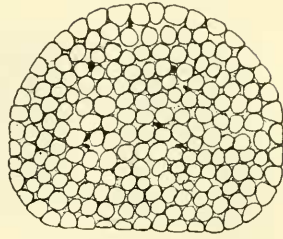
- FIG. 1. *Magnadigita torresi*. View of dorsal surface of gland-cluster,  $\times 12$ .  
FIG. 2. *Magnadigita pesrubra*. View of dorsal surface of gland-cluster,  $\times 10$ .  
FIG. 3. *Magnadigita nigroflavescens*. View of dorsal surface of gland-cluster,  $\times 12$ .  
FIG. 4. *Magnadigita subpalmata*. View of dorsal surface of gland-cluster,  $\times 12.5$ .  
FIG. 5. *Magnadigita robusta*. View of dorsal surface of gland-cluster,  $\times 12$ .  
FIG. 6. *Magnadigita nigroflavescens*. Longitudinal cross-section,  $\times 54$ .



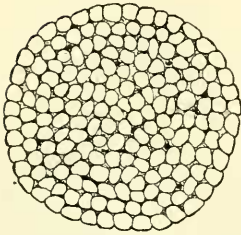
PLATE IV



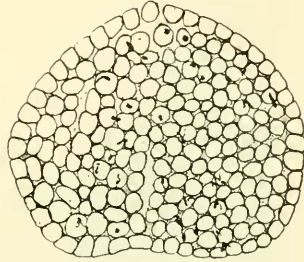
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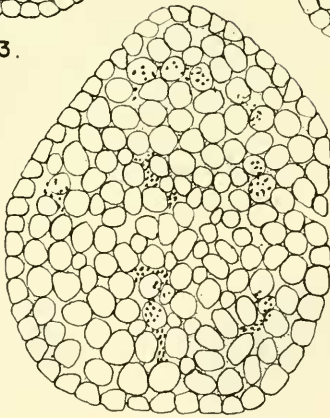
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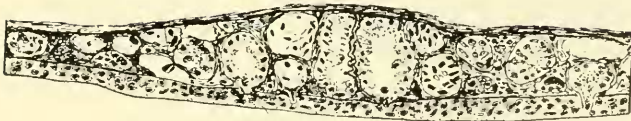
3.



4.



5.



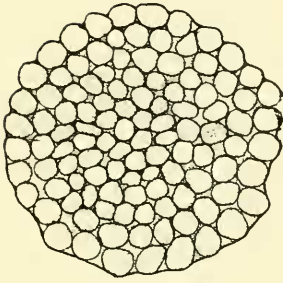
6.

## PLATE V

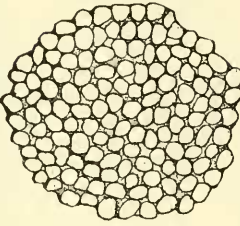
The Mental Hedonic Gland-clusters of the Genus *Thorius*.

- FIG. 1. *Thorius narisovalis*. View of dorsal surface of gland-cluster,  $\times 39$ .  
FIG. 2. *Thorius pulmonaris*. View of dorsal surface of gland-cluster,  $\times 35$ .  
FIG. 3. *Thorius macdougalli*. View of dorsal surface of gland-cluster,  $\times 33$ .  
FIG. 4. *Thorius sp.* View of dorsal surface of gland-cluster,  $\times 35$ .  
FIG. 5. *Thorius pennatulus*. View of dorsal surface of gland-cluster,  $\times 33$ .  
FIG. 6. *Thorius dubitus*. View of dorsal surface of gland-cluster,  $\times 40$ .  
FIG. 7. *Thorius troglodytes*. View of dorsal surface of gland-cluster,  $\times 37$ .  
FIG. 8. *Thorius narisovalis*. Longitudinal cross-section,  $\times 113$ .

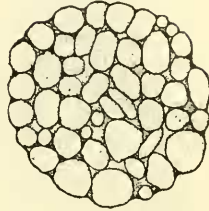
PLATE V



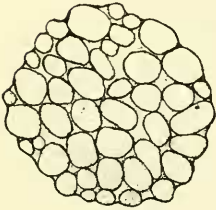
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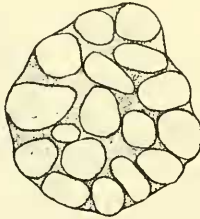
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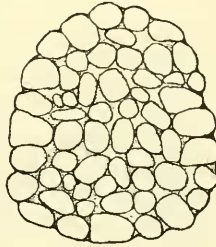
3.



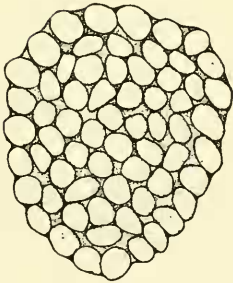
4.



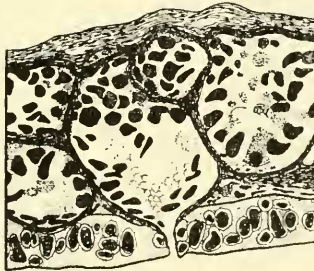
5.



6.



7.



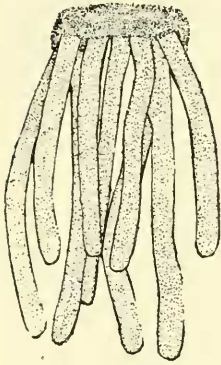
8.

## PLATE VI

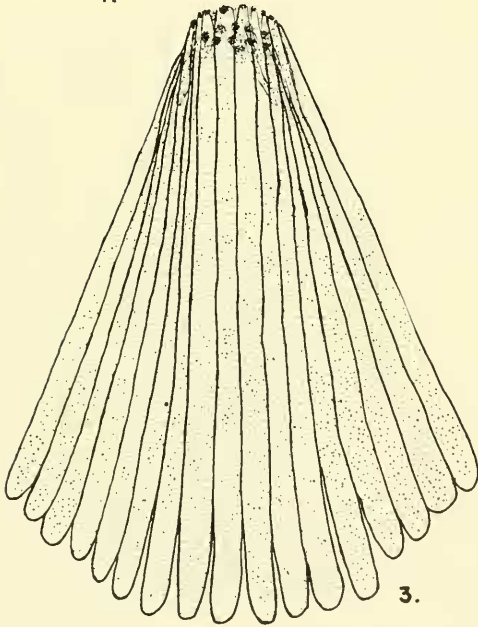
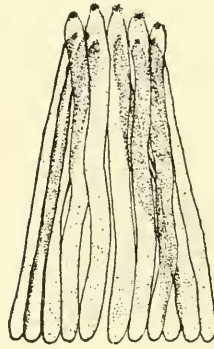
The Mental Hedonic Gland-clusters of the Genus *Oedipina*

- FIG. 1. *Oedipina cyclocauda*. View of dorsal surface of gland-cluster,  $\times 32$ .  
FIG. 2. *Oedipina uniformis*. View of dorsal surface of gland-cluster,  $\times 34$ .  
FIG. 3. *Oedipina bonitaensis*. View of dorsal surface of gland-cluster,  $\times 50$ .  
FIG. 4. *Oedipina bonitaensis*. Lateral view of gland-cluster,  $\times 50$ .  
FIG. 5. *Oedipina cyclocauda*. Longitudinal cross-section,  $\times 96$ .

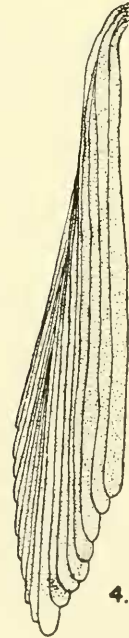
PLATE VI



1.



3.



4.



5.